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With Six Plates, and Five Figures in Text.

(Continued from page 3 of cover.)

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ON THE DEVELOPMENT OF THE CORAL *AGARICIA FRAGILIS* DANA.[1]

By J. W. Mavor.

Presented by E. L. Mark. Received June 15, 1915.

CONTENTS

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[1] Contributions from the Bermuda Biological Station for Research. No. 38.

1. Introduction.

Interest has been re-awakened of recent years in the development of the *Hexacorallidae* by the papers of Duerden (:04), who has established the order of development of the mesenteries in the larva and of the septa in the attached polyp. As regards the larval development his work agrees in the main with that of Wilson ('88) on *Manicina areolata.* In the skeleton Duerden is the first to find bilateral symmetry in the order of development of the primary exosepta. Our knowledge of the development of coral larvae is in the main confined to four species; *Astroides calycularis* (Lacaze-Duthiers '73); *Manicina areolata* (Wilson '88); *Caryophyllia cyathus* (Von Koch '97) and *Siderastrea radians* (Duerden :04). The early development of the skeleton has been studied in *Astroides calycularis* by Lacaze-Duthiers ('73), in *Caryophyllia cyathus* by Von Koch ('97), in *Caryophyllia clavus, C. smithii* and *Balanophyllia regia* by Lacaze-Duthiers ('97) and in *Siderastrea radians* by Duerden (:04).

In 1907 the writer went to the Bermuda Biological Station for the purpose of studying the development of a recent coral.[2] He was fortunate enough to find the common "hat" or "shade" coral, *Agaricia fragilis,* breeding and was able to rear the larvae.

As the development of the primary mesenteries of the larvae of corals has been worked out in comparatively few cases and a study of the soft parts seemed a necessary prelude to a study of the skeleton, free swimming larvae have been studied both in the living state and in paraffin sections. These observations form the first part of the paper. The writer was not very successful in rearing the young polyps. In consequence only a few skeletons were obtained. The second part of the paper is devoted to a description and discussion of these young skeletons.

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[2] The writer wishes to express his indebtedness to Dr. E. L. Mark for kind assistance and criticism while at the Biological Station and later in the Zoölogical Laboratory of Harvard University.

PART I. ON THE LARVAL DEVELOPMENT.

1. General Considerations.

a. *Breeding Season.*

The first larvae of *Agaricia fragilis* were obtained from a colony of the coral collected in a cave on the shore of Agar's Island, Bermuda, on July 8th, 1907. The colony, which was about eight or nine centimeters in diameter, was brought to the laboratory in the morning and placed in fresh sea water in a battery jar. In the afternoon numerous pear-shaped, light brown, larvae were seen swimming about in the water. Other colonies collected from a cave on Tucker's Island on July 15th when placed in fresh sea water in the laboratory gave off similar larvae. In 1908 larvae were obtained from seven out of eleven colonies over 5 cm. in diameter collected from Long Island, Bermuda, between the 22nd and 30th of June. No larvae were obtained from nine colonies under 5 cm. in diameter collected on June 21st and 22nd from the same place.

These observations show that *Agaricia fragilis* may be found breeding at the Bermuda Islands during the latter part of June and the first part of July.

b. *Extrusion of the Larvae.*

For the purpose of obtaining the larvae, adult colonies of *Agaricia fragilis* were collected in caves and brought to the laboratory in battery jars. During the transference to the laboratory it is probable that in many cases the temperature of the water containing the coral was raised above the temperature of the water in the cave. Larvae were often extruded in large numbers while the corals were being transported to the laboratory and during the few hours immediately succeeding this. What the factors were which produced their extrusion was not determined. Usually, however, not all of the larvae were extruded at this time, a certain number being seen to remain within the parent colony.

c. *Form of the Larva.*

The planula, which is light brown in color, is capable of considerable change of form. It may, however, be described as piriform, the

broader, rounded end being aboral and in advance during swimming, while the oral opening is situated at the more pointed posterior end. The alterations in form may be of two kinds; first, elongation, with corresponding decrease in the radial axis, or shortening, with corresponding increase in the radial axis; or, secondly, a contraction of one side of the planula so that the aboral end, which in such cases is usually somewhat flattened, becomes turned to one side. In *Siderastrea radians* Duerden (:04) found the broad rounded end of the larva to be the oral end.

The elongated form is the one usually assumed by the larva when swimming rapidly through the water. The larva takes a more definitely piriform shape when it swims slowly over the substratum. In the latter case there may be a slight in-pushing of the aboral end forming a hollow in the center. This hollowing out of the center suggests a mechanism working by suction. When the larva comes to rest and applies itself to the substratum, it becomes hemispherical, the aboral end being the flat side of the hemisphere and applied to the substratum. Later these larvae may become almost disk shaped. In the preserved specimens the shape is usually either piriform or almost hemispherical. After having become hemispherical and applied to the substratum, the planula may detach itself, elongate and swim away.

d. Fixation.

The planula swims with the broader, rounded, aboral end foremost, as already stated, rotating on its longitudinal axis as it does so. In *Siderastrea radians,* which has the mouth at the broader end of its piriform larva, Duerden (:04) found that, as is the case in *Agaricia fragilis,* the aboral end is kept in front. From this it would seem that while the form of the larva of Siderastraea is favorable for locomotion that of *Agaricia* must satisfy other conditions than that of offering the least resistance to forward motion.

Larvae after they are expelled from the parent colony are usually elongated in shape and swim through the water rapidly. Later they become shorter and broader and swim more slowly. The normal course seems to be for them to affix themselves to the substratum within a few hours after they have been extruded. In the laboratory larvae which did not become fixed in about twenty-four hours after extrusion did not do so when kept for seven days, although during this time they continued to swim through the water and also, as flat

disks, to move over the substratum with the aboral end downwards. The failure of such larvae to become attached may have been due to the surface of the glass vessel being unsuitable for fixation. As, however, some of the larvae became fixed on glass while others did not attach themselves even to rough surfaces, such as stones placed in the vessel, the nature of the substratum does not seem to have been the only factor involved. The experiment was tried of keeping larvae in the dark and also under additional pressure,— eighteen inches of water,— but in both cases they failed to attach themselves.

When the larva is about to fix itself it becomes flattened and its aboral end is applied to the substratum. If a stream of water from a pipette be forced against such a larva, the animal may be made to elongate its body again, provided it has not begun the formation of a skeleton. Such larvae may remain in the current of the pipette, appearing as if attached to the surface of the glass by an elastic strand. This suggests that an adhesive mucous substance may be secreted at the aboral end when it becomes applied to the glass. In the free-swimming piriform larvae, especially when they are swimming close to the substratum and apparently in a condition to affix themselves, a concavity may be seen at the aboral end, giving that end the appearance of a suction disk.

Sometimes larvae flattened themselves out into disks at the surface of the water. Such larvae never attached themselves to the bottom or sides of the glass jar and almost all the individuals of such lots became flattened out under the surface of the water. Such larvae tended to fuse into "aggregations" (Duerden :04) and also to go to the sides of the vessel (surface tension). Many of these larvae lived to secrete a skeleton with six well developed primary septa while still floating at the surface of the water.

2. Anatomy.

a. *Material, Methods and General Features.*

A considerable number of larvae, fixed in various mixtures, were embedded in paraffin and sectioned either transversely or parallel to the oral-aboral axis. Transverse sections were found to be by far the most suitable for the study of the general structure. Nine of the larvae so sectioned have been selected for detailed description in order that the reader may have in as concrete a form as possible the data on

which the conclusions of the paper are based. Although only individual differences have been observed between the opposite sides of the bilaterally symmetrical planulae, it has been thought best for convenience in description to distinguish a right and a left side. In this connection the aboral end of the planula, which is foremost in locomotion, has been considered anterior while the oral end is considered posterior.

Each larva was cut into a series of transverse sections of equal thickness, which varied from 5 μ to 7 μ for the different series. In recording the position of structures in the larvae the thickness of the sections has been used as a unit of measure.

The nine larvae fall into four groups:— First, larva A, which has four pairs of mesenteries, only two of which are well developed; Second, larvae B, C, D, and E, in which there are six pairs of mesenteries, the fifth and sixth however being only slightly developed and the mesenterial filaments not extending the whole length of the larva; Third, larvae F, G and H, in which all six mesenteries are well developed and the mesenterial filaments of the first two pairs of mesenteries extend through the greater part of the larvae; Fourth, larva I, in which, besides the greater development of the fifth and sixth pairs of mesenteries, there are developed mesenterial filaments on the third pair of mesenteries.

The musculature of the mesenteries consists of fibres developed in endoderm cells where these abut on the mesogloea. These fibres stain deeply with haematoxylin and so are easily distinguished in the preparations. In the mesenteries the majority of these fibres run longitudinally. Some, however, especially those near the junction of the mesogloea of the mesentery with that of the body wall, run obliquely or even transversely. It is not always easy to determine which side of the mesentery shows the large number of fibres; first, because the mesogloea in the mesenteries is usually very thin and does not take stain well, and, secondly, because there are always some fibres on each side. This is still more difficult in the newly formed mesenteries, as in these there is almost always an approximately equal number of fibres on each side of the mesentery. The distribution of the muscle fibres given in the diagram (text Fig. 1, *C*) is based on careful examination with a 2-mm. apochromatic objective and compensating oculars x8 and x12. In the first and second pairs of mesenteries the muscle fibres are confined almost entirely to the ventral sides. In the third and fourth pairs, the directives, the muscle fibres are more numerous on the lateral sides. In the fifth

and sixth pairs, when a difference can be observed between the two sides of the mesenteries, the fibres are most numerous on the dorsal side (Fig. 2, *E*). In the mesenteries in which a mesenterial filament is developed (first and second pair), the muscle fibres are most numerous in that region of the mesentery which is about twice as far from the body wall as from the internal margin of the mesentery, in those sections in which the filament appears. In all other cases the muscle fibres are most numerous along the internal edges of the

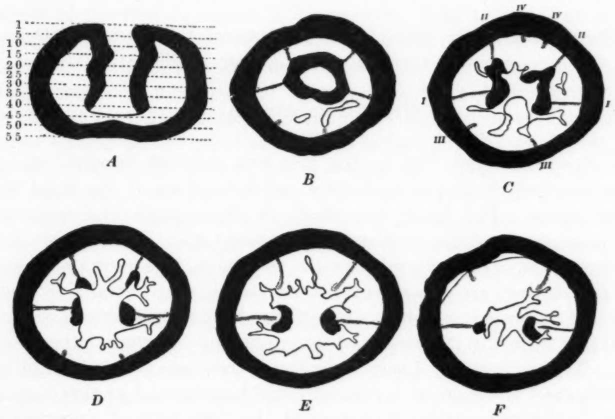

FIGURE 1. *Agaricia fragilis.* Larva A. *A*, a longitudinal section through the first pair of mesenteries and their filaments, reconstructed from transverse sections. Viewed from the dorsal side. The numbers, and the dotted lines corresponding to them, indicate the numbers and positions of the transverse sections of the series. Ectoderm and mesoderm black. *B, C, D, E,* and *F* represent sections number 14, 18, 23, 30 and 41, respectively. The reader views the aboral face of the section, and dorsal is up, so that the right of the larva is on the left of the figure. In *C, I, II, III, IV* indicate the first, second, third and fourth pairs of mesenteries, respectively. × 90.

mesenteries and are usually numerous on both sides of the mesentery along this edge.

The musculature of the body wall consists of a layer of longitudinal fibres developed in the inner ends of the ectoderm cells where they abut on the mesogloea and of a layer of circular muscles developed in the endoderm cells where they reach the mesogloea of the body wall. The mesoderm of the body wall, although thin, is everywhere clearly to be seen.

At the oral end the ectoderm of the body wall is folded in to form the oesophagus and the filaments of the first two pairs of mesenteries. At its oral end the oesophagus forms a complete tube. Aborally it becomes divided dorsally so that it extends for some distance as a scoop-shaped structure, U-shaped in cross section. In the following descriptions the point where the oesophagus ceases to be a complete tube and becomes scoop-shaped is expressed by saying that it is interrupted dorsally.

b. Description of the Mesenteries, Mesenterial Filaments and Gastro-vascular Cavities of the Larvae Studied.

Group I. Larva A.

In this larva (text, Fig. 1) the first two pairs of primary mesenteries are well developed and there are indications of the third and fourth pairs. The larva was fixed in Flemming's chromo-aceto-osmic mixture and the sections were stained with Heidenhain's iron haematoxylin. The aboral end of the larva was sectioned first and the sections are almost exactly transverse, the ventral side of the oral end, however, extends six sections beyond the dorsal side, a deviation from the transverse which cannot be detected at the aboral end. The sections are 7 micra thick and there are 56 of them in all. Text-figure 1 shows at *A*, a reconstructed longitudinal section passing through the mesenterial filaments of the first pair of mesenteries. The horizontal dotted lines are drawn in the planes of sections and each of the numbers at the side of the figure indicates the number of the section to which the line corresponds, beginning with the oral end. The figure shows that the aboral end of the larva is flattened and contains a slight concavity. This shape may be due to contraction on the application of the fixing fluid, but larvae of this form were observed in the living state. At *B, C, D, E,* and *F,* in Figure 1, are shown the 14th, 18th, 23rd, 30th, and 41st sections respectively from the oral end. Photomicrographs of sections 15, 24, 30, and 46 are shown in Plates **1** and **2**.

The oesophagus is irregularly circular in cross section (Fig. 1, *B*) and extends aborally in the axis of the larva. The fact that it appears nearer to the dorsal side in the figure is due to the section having been cut somewhat obliquely. The larva has been cut so that the oesophagus appears as a complete tube first in section 6, the ventral side

only appearing in the earlier sections. In section 8 the endoderm appears on the ventral side and in section 14 on the dorsal side for the first time. The oesophagus is interrupted first ventrally in section 16 and then dorsally in section 19. In the sections the oesophagus is cut obliquely on the ventral side while on the dorsal side it is sectioned transversely. In spite of this the oesophagus extends on the ventral side through 12 sections, while on the dorsal side it extends through only 6 sections.

Although interrupted on the ventral side, the ectoderm of the oesophagus is continuous with the ectoderm of the mesenterial filaments of the first two pairs of mesenteries (Fig. 1, *C*). The mesenterial filaments of mesenteries *I* and *II* of the right side of the larva, (left side of the figure) are fused together as far as section 19, after which they become separated; those of the left side are fused as far as section 21. The mesenterial filaments of the first pair of mesenteries extend on the right side of the larva as far as section 43; on the left side of the larva as far as section 41. They are larger than the filaments of the second pair of primary mesenteries and there is no evidence of an aboral enlargement as found in the larvae of the later stages. The mesenterial filaments of the second pair of mesenteries extend on the left side into section 28 and on the right side into section 34. The mesenteries of the first pair extend on the right side of the larva from section 9 to 46, and on the left side from section 11 to 48. Those of the second pair extend on the right from section 13 to 46, on the left from section 14 to 46. The beginning of the development of the third pair of mesenteries appears on the right of the larva between sections 8 and 31 and on the left between sections 10 and 27. At their oral ends the third pair of mesenteries extends to the ectoderm of the oesophagus. Slight indications of the fourth pair of mesenteries are found on either side in sections 12 to 18 (Fig. 1, *C*). Here also the mesentery as defined by mesoglea and muscles extends to the ectoderm of the oesophagus. The distance to which the muscles and mesoglea of the fourth pair of primary mesenteries extend into the endoderm is less than in the third pair.

Group II. Larva B.

This larva has six pairs of mesenteries all clearly shown. It was fixed in a saturated solution of corrosive sublimate to which 1% acetic acid was added, and the sections were stained in Heidenhain's iron

haematoxylin and congo red. The sections deviate very slightly from the transverse, the right dorsal side of the oral end of the larva being cut first. As the oral end was cut first the right side of the larva is to the right in the preparation. The sections are 7 μ in thickness and there are 57 of them in all. As in the previous larva, the aboral end is somewhat flattened.

The oesophagus is circular in cross section, and extends on the ventral side through one more section than on the dorsal side. On the ventral side it extends into section 22. After leaving their junction with the oesophagus in section 22 the mesenterial filaments of the first and second mesenteries of either side are not fused as in larva A. Those of the first pair of mesenteries extend on either side into section 42 and those of the second pair are turned from the aboral end of the oesophagus outwards toward the oral end of the larva extending on the right into section 12 and on the left into section 17. The filaments of the first pair of mesenteries are enlarged on the right side between sections 30 and 37, and on the left side between sections 37 and 39, those of the second pair of mesenteries decrease gradually in size until they end. Only mesenteries *I* and *II* are complete.

The lengths and positions of the mesenteries are given in the following table, which shows the number of the section where each mesentery begins and ends:

Number of mesentery	*I*	*II*	*III*	*IV*	*V*	*VI*
Right side of larvae						
Oral end section No.	7	9	10	11	8	7
Aboral end section No.	45	38	44	36	44	31
Left side of larvae						
Oral end section No.	11	11	12	11	12	12
Aboral end section No.	48	40	44	36	44	36

Although traces of the fifth pair of mesenteries extend into section 44 these mesenteries are only slightly developed in the aboral half of the larva.

Group II. Larva C.

This larva is in about the same stage of development as larva B, but the fifth and sixth pairs of mesenteries show more clearly. It was fixed in a saturated solution of corrosive sublimate plus 1% acetic acid. The 90 sections were stained with Heidenhain's iron haematoxylin and congo red, each being 5 μ thick. The aboral end

of the larva was cut first and on the dorsal side, so that the ventral side of the oral end occurs in nine sections after the dorsal side has ceased to appear.

The oesophagus is almost round in cross section and is shorter on the dorsal side than on the ventral side, the length of the dorsal side being approximately 50 μ, while that of the ventral side is 170 μ.

The mesenterial filaments of the first and second pairs of mesenteries are continuous with the ectoderm of the oesophagus. On the right side they are fused in section 24 but below that separate, the filament of the first mesentery extending into section 64, that of the second into section 57. On the left side they are fused as far as section 45, below which the filament of the first mesentery extends as far as section 63; the second mesentery has no separate mesenterial filament. The filaments of the first pair of mesenteries are enlarged and crescent shaped in cross section on the right between sections 43 and 61 and on the left between sections 40 and 59. The filaments of the second pair of mesenteries are not thus enlarged and are approximately uniform in cross section throughout their length.

The lengths and positions of the mesenteries are given in the following table:

Number of mesentery	*I*	*II*	*III*	*IV*	*V*	*VI*
Right side of larva						
Oral end section No.	15	16	7	20	12	20
Aboral end section No.	69	74	55	82	47	66
Left side of larva						
Oral end section No.	11	16	7	20	8	21
Aboral end section No.	68	74	55	82	47	66

Only mesenteries *I* and *II* are complete.

Group II. Larva D.

Larva D, which was in nearly the same stage of development as larvae B and C, was fixed in a saturated solution of corrosive sublimate, and the sections were stained in Mallory's phosphotungistic acid haematoxylin. The plane of sectioning deviated slightly from the transverse, the first part of the larva cut being slightly dorsal to the middle of the right side. The 47 sections are each 7 μ thick.

The oesophagus is elliptical in cross section, the long axis being dorso-ventral.

The mesenterial filaments of the first and second pairs of mesenteries of the right side are not fused together after they leave the oesophagus. The first of these extends from sections 13 to 26, the second from sections 13 to 25. On the left side the filaments are fused from their junction with the oesophagus at section 13 as far as section 17, below which the filament of the first mesentery extends to section 29, that of the second to section 25. The filaments of the mesenteries are enlarged as follows: those of the first pair on the right between sections 19 and 22, on the left between sections 18 and 23, those of the second pair on the right between sections 19 and 23, on the left between sections 18 and 21.

The length and position of the mesenteries is shown in the following table:

Number of mesentery	*I*	*II*	*III*	*IV*	*V*	*VI*
Right side of larva						
Oral end section No.	7	6	9	6	14	5
Aboral end section No.	35	31	38	34	37	34
Left side of larva						
Oral end section No.	9	10	9	7	13	18
Aboral end section No.	44	39	40	34	42	38

Only mesenteries *I*, *II* and *III* are complete.

Group II. Larva E.

This larva was fixed and stained like larva D. The aboral end was cut first and the sections are so nearly transverse that all sides of the circular oesophagus appear in the next to the last section of the series. There are 55 sections, each 7 μ thick and they are numbered from the *oral* end.

The oesophagus is elliptical in cross section. Its dorsal side ends at section 7 and its ventral side at section 11.

The mesenterial filaments of the first and second pairs of mesenteries are separate where they leave the oesophagus. The filaments of the first pair extend on either side from the oesophagus, at section 11, to section 47. Those of the second pair extend on the right to section 31 and on the left to section 35. The filaments of the first pair are enlarged in cross section on both sides between sections 23 and 44. Those of the second pair on the right between sections 16 and 29 and on the left between sections 16 and 34.

The position and extent of the mesenteries is shown in the following table:

Number of mesentery	*I*	*II*	*III*	*IV*	*V*	*VI*
Right side of larva						
Oral end section No.	4	4	5	5	6	6
Aboral end section No.	49	49	49	44	49	44
Left side of larva						
Oral end section No.	6	6	5	5	9	9
Aboral end section No.	50	49	51	44	50	44

In section 49 mesenteries *I* and *II* of the right side are united at their internal ends. Only mesenteries *I* to *IV* are complete.

Group III. Larva F.

This larva (text, Fig. 2) is not so much contracted along its oral-aboral axis as the one last described, and the oesophagus is only slightly invaginated. It was fixed in a saturated solution of corrosive sublimate and the sections stained in Mallory's phosphotungstic acid haematoxylin. The oral end of the larva was cut first. The sections are almost exactly transverse. The oesophagus appears as a complete circle of ectoderm in the third section, the first two sections showing the dorsal side only. The sections are 6 μ thick and there are 86 of them. Of the sections, Figure 2, *A–I*, shows numbers 9, 13, 18, 21, 33, 45, 61, 71 and 74 and Plates 3 and 4 show photomicrographs of numbers 12, 17, 61 and 73.

The oesophagus is elliptical in cross section, the long axis being dorso-ventral. It ceases on the dorsal side at section 9 (Fig. 2, *A*). Below this its cross section is U-shaped until section 13 (Fig. 2, *B*) is reached. Below section 13 it is interrupted on the ventral side also. The invaginated ectoderm of the right side of the larva is joined by the first, second and third mesenteries, that of the left side is joined by the first and second mesenteries (Fig. 2, *C*).

Below section 20 the ectoderm is continued on both sides as the separate mesenterial filaments of the first and second pairs of mesenteries. The filaments of the first pair extend on the right as far as section 70 and on the left as far as section 73, which is practically the whole extent of the gastrovascular cavity. The filaments of the second pair extend on both sides as far as section 56. The mesenterial filaments are enlarged as follows: those of the first pair of mesenteries on the right between sections 49 and 66, on the left between sections 52 and 70, those of the second pair of mesenteries on both sides between sections 32 and 54 (Fig. 2, *E–H*).

The six pairs of primary mesenteries extend practically the whole

length of the endoderm of the larva. The following table shows their positions and extent:

Number of mesentery	*I*	*II*	*III*	*IV*	*V*	*VI*
Right side of larva						
Oral end section No.	8	8	9	8	9	13
Aboral end section No.	75	75	72	70	72	75
Left side of larva						
Oral end section No.	9	8	9	8	10	12
Aboral end section No.	77	76	72	70	72	77

Only mesenteries *I* to *IV* are complete.

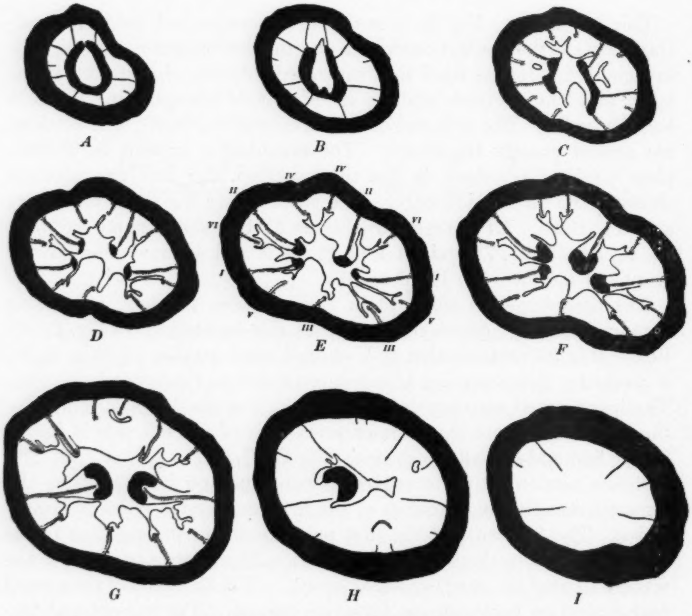

FIGURE 2. *Agaricia fragilis*. Larva F. Transverse sections the oral end having been cut first. The right of the larva is to the right in the figures. Ectoderm and mesoglea colored black. *A, B, C, D, E, F, G, H, I* sections number, 9, 13, 18, 21, 33, 45, 61, 71, and 74, respectively. In *E*, *I*, *II*, *III*, *IV*, *V* and *VI* mark the first, second, third, fourth, fifth, and sixth sections. × 90.

Group III. Larva G.

The chief differences between this larva and larva F pertain to the form of the oesophagus and gastrovascular cavity. It was fixed in Flemming's fluid and stained with Heidenhain's iron haematoxylin. The series consists of 154 transverse sections each 7 μ thick. The aboral end was cut first, so that the sections are viewed from this end, but the numbering of the sections is from the oral end.

The oesophagus is well invaginated and is circular or slightly oval in cross section (Fig. 3, *A*) as far as section 20. It is then interrupted on the dorsal side, as seen in sections 21–23 (Fig. 3, *B*), after which the ectoderm becomes divided also on the ventral side. The slight deviation of the sections from the true transverse plane is such that their ventral edges are more aboral than their dorsal edges, a fact which can be learned from the table showing the extent of the mesen-

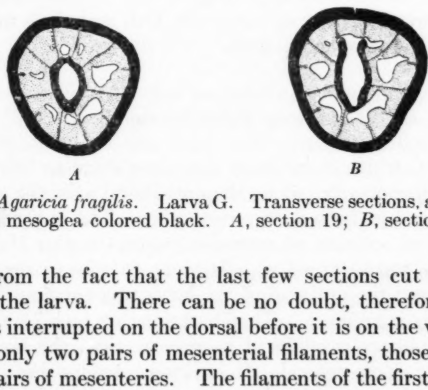

FIGURE 3. *Agaricia fragilis*. Larva G. Transverse sections, aboral aspect. Ectoderm and mesoglea colored black. *A*, section 19; *B*, section 23. $\times$ 90.

teries, and from the fact that the last few sections cut the ventral side only of the larva. There can be no doubt, therefore, that the oesophagus is interrupted on the dorsal before it is on the ventral side.

There are only two pairs of mesenterial filaments, those of the first and second pairs of mesenteries. The filaments of the first and second mesenteries are fused on the left from sections 24 to 31 and on the right from sections 24 to 33. The sections of the filaments of the first pair of mesenteries decrease in size until section 57 is reached, after which they increase in size on both sides up to about section 124, where they are somewhat larger than those of the second pair of mesenteries. After this they decrease in size till they end, on the right at section 135 and on the left at section 132. The filaments of the second pair of mesenteries increase in size up to about section 57. In section 40 they have about the same size as those of the first pair of mesenteries

in that section. From sections 57 to 61 the size remains nearly constant, but below this it decreases until they end, on the right at section 106 and on the left at section 102.

The extent and position of the mesenteries is shown in the accompanying table.

Number of mesentery		*I*	*II*	*III*	*IV*	*V*	*VI*
Right side							
	Oral end section No.	13	14	9	12	12	14
	Aboral end section No.	144	147	139	135	142	142
Left side							
	Oral end section No.	8	9	7	11	8	8
	Aboral end section No.	138	135	138	134	137	133

Only mesenteries *I* to *IV* are complete.

The gastrovascular cavity extends orally between the mesenteries as in larva B. At the oral end however it is found between the first four pairs of mesenteries only (Fig. 3, *A*). Where these diverticula of the gastrovascular cavity occur the fifth and sixth mesenteries do not reach to the oesophageal wall.

Group III. Larva H.

This larva, which is in about the same stage as larvae F and G, is very much contracted along the oral-aboral axis, the aboral surface being retracted to form a deep concavity. The individual was fixed in a saturated solution of corrosive sublimate plus 1% acetic acid. The sections were stained with Heidenhain's iron haematoxylin and congo red, and the oral end of the larva was cut first, the right side being slightly in advance. The 71 sections are each 7 μ thick.

The oesophagus is elliptical in cross section, the long axis of the ellipse being dorso-ventral. It is interrupted on the dorsal side in section 14 and on the ventral side in section 21, its ventral side extending therefore 7 sections beyond its dorsal side.

The mesenterial filaments of the first and second pairs of mesenteries, the only ones present, extend nearly the whole length of the larva, almost but not quite touching the mesoglea of the aboral end; their position is as follows: those of the first pair of mesenteries on the right reach from section 22 to section 41, and on the left from section 23 to section 44; those of the second pair of mesenteries on the right reach from section 22 to 41 and on the left from section 23

to 41. The filaments of the same side are not fused, as in some previous larvae, except that on the left side they are united at their origin, (section 23). The enlargement of the filaments of the first pair of mesenteries reaches from section 29 to 38; the sections of the second pair are of almost uniform size throughout their length.

The mesenteries extend practically the entire length of the larva; their positions are shown in the following table:

Number of mesentery	*I*	*II*	*III*	*IV*	*V*	*VI*
Right side of larva						
Oral end section No.	8	7	9	7	17	17
Aboral end section No.	52	49	54	50	53	51
Left side of larva						
Oral end section No.	10	9	10	7	17	17
Aboral end section No.	56	54	56	51	56	55

Mesenteries *I* to *IV* are the only complete ones.

Group IV. Larva I.

This larva is slightly larger than any of the previous ones, and shows an advance in the development of the primary mesenteries and of the mesenterial filaments. It was fixed and stained like larva G, and then cut into 133 transverse sections, each 5 μ thick, the aboral end being cut first. Figure 4 (*A–F*) shows the 15th, 19th, 23rd, 25th, 73rd and 93rd sections. Photomicrographs of sections 19 and 26, are shown on Plate **5** and of 73 and 93 on Plate **6**.

The oesophagus is slightly more invaginated than in larva B. It is oval in cross section (Fig. 4, *A*) from the oral end to section 17. In section 17 it is U-shaped, the ectoderm being interrupted on the dorsal side. This is also the case in section 19 (Fig. 4, *B*). Beyond this section the ectoderm is interrupted also on the ventral side (Fig. 4, *C*). On the ventral side of the oesophagus in sections 16 to 19 a diverticulum of the gastrovascular cavity extends forward in the region of the third pair of mesenteries (Fig. 4, *B*). The mesenterial filaments of the first and second mesenteries (Fig. 4, *D*) are fused on the right (left as seen in the figures) as far as section 29, on the left as far as section 38.

The mesenterial filaments of the first pair of mesenteries extend on both sides into section 112. The transverse sections of these filaments are smaller than those of the filaments of the second pair of

mesenteries as far as section 80 on the right and on the left up to section 83. They are largest (Fig. 4, *F*) on the right between sections 87 and 108 and on the left between sections 87 and 110, where they are larger than any of the transverse sections of the filaments of the second pair of mesenteries. The mesenterial filaments of the second pair of mesenteries extend on the right into section 89 and on the left (Fig. 4, *F*) into section 95. The transverse sections of these filaments (Fig. 4, *E*) are largest on the right between sections 54 and 87 — where

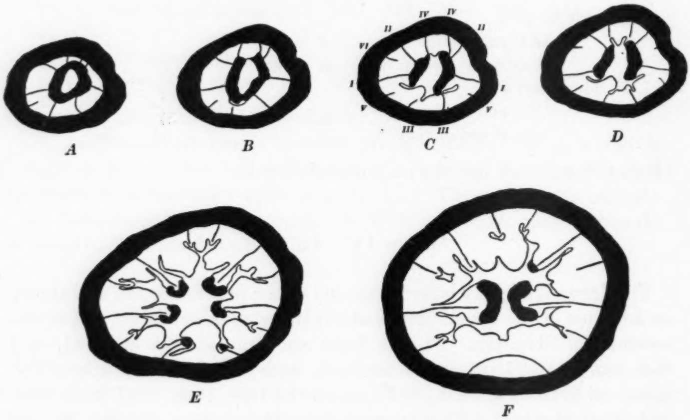

FIGURE 4. *Agaricia fragilis*. Larva I. Transverse sections of larva, the oral end having been cut first. Dorsal being up, the right of the larva is to the right in the figures. Ectoderm and mesoglea colored black. *A, B, C, D, E, F*, sections number 15, 19, 23, 25, 73, 93 respectively. In *C*, *I, II, III, IV, V, VI* mark the first, second, third, fourth, fifth, and sixth pairs of mesenteries. × 90.

up to section 80 they are larger than the filaments of the first pair of mesenteries in the same sections,— and on the left between sections 58 and 90, where they are larger than the filaments of the first pair of mesenteries as far as section 83. The filament of mesentery *III* on the right side of the larva (left in the preparation) is not continuous with the ectoderm of the oesophagus, being absent in sections 20 to 26. On the left side of the larva the filament of the corresponding mesentery if present at all is reduced to a few scattered cells in these sections. Both filaments are enlarged beyond these sections but are always much

smaller than the filaments of mesenteries *I* and *II*. The filament on the left of the larva (right in the sections) extends to about section 73 (Fig. 4, *E*), that on the right of the larva to about section 77, the limits not being sharply defined.

The filaments of mesenteries *III* differ histologically from those of *I* and *II*. The ciliated cells are shorter and thicker and gland cells seem to be absent, resembling in this the endoderm cells, from which the filament is not always sharply to be distinguished.

A table is given showing the extent of the six primary mesenteries in this larva.

Number of mesentery	*I*	*II*	*III*	*IV*	*V*	*VI*
Right side of larva						
Oral end section No.	9	12	9	15	13	23
Aboral end section No.	115	112	102	104	112	102
Left side of larva						
Oral end section No.	12	15	11	15	21	26
Aboral end section No.	115	112	102	104	112	102

Only mesenteries *I* to *IV* are complete.

This table shows that all of the mesenteries extend practically the whole length of the larva. The third and fourth mesenteries are, however, considering their early appearance in development, somewhat shorter than the others. The mesoglea of the mesenteries is very thin and in many cases can be seen only where it is cut obliquely. That it is somewhat tough and rigid, at least in fixed and stained preparations, is shown by its being slightly displaced in sections, leaving the less resistant entoderm cells behind it.

The gastrovascular cavity is clearly in the process of being divided into compartments corresponding to the mesenteries. It will be noticed in Figure 4, *E* and *F*, that a cleft in the entoderm occurs on either side of each mesentery and that entoderm bulges inward between the mesenteries and between these clefts. This would seem to indicate that the formation of the compartments is brought about by the formation of the mesenteries. There is evidence in the histology of the entoderm that the clefts referred to are formed by the separation and breaking down of cells rather than by a process of infolding. This would tend to support the theory that the clefts are due to the closer adherence of the contiguous entoderm cells to the more rigid mesoglea of the mesenteries.

c. Conclusions as to the Course of Development of the Mesenteries, Mesenterial Filaments and the Gastrovascular Cavity.

If the assumption be made that the mesenteries develop in the order of their size, the order of their development in the larva of *Agaricia fragilis* is indicated by the numbers given the mesenteries (Fig. 2, *E*), with the exception, that numbers V and VI develop simultaneously. So far as the first four pairs of mesenteries are concerned the order of development is that found by Faurot ('95) in *Adamsia palliata* and *Halcampa chrysanthellum;* by Wilson ('88) in *Manicina areolata;* by McMurrich ('91) in *Rhodactis sancti-thomae* and *Aulactinia* and by Duerden (:04) in *Siderastrea radians.*

The writer believes that the larvae studied show that in the development of the six pairs of primary mesenteries there may be recognized three periods as follows: first, a period in which there are two pairs (*I* and *II*), a condition not represented by any of the larvae, but shown probably to exist by the great development of pairs *I* and *II* and the only slight indication of pairs *III* and *IV* in larva A; second, a period in which there are four pairs, represented in an early stage by larva A, and shown probably to exist by the large size of pairs *III* and *IV* and the small size of pairs *V* and *VI* in larvae B and C; third, a period in which there are six pairs of mesenteries represented by larvae B to I. By dividing the development of the mesenteries into these periods the writer does not wish to deny the appearance of the pairs of mesenteries in succession, but merely to show their association into three sets of two pairs each. Further, it is to be noticed that this association in sets of two pairs becomes more intimate as development proceeds. In larva A pair *I* shows a very considerable advance over pair *II* and this difference persists to some extent in the older larvae. In the same larva pair *III* shows only a slight advance over pair *IV* and in the older larvae such a difference between pairs *III* and *IV* is hardly to be seen. In larvae B to I pairs *V* and *VI* seem to have appeared and developed simultaneously.

If this interpretation is correct, the ventro-dorsal order of development which is evident in the first two pairs, becomes less marked in the next two pairs (*III* and *IV*) and has entirely disappeared in the last two pairs (*V* and *VI*). In other words the bilateral symmetry of the larval mesenteries has begun to give way to a radial symmetry while it is still free swimming.

Evidence of close association in development between the first two pairs of mesenteries is seen also in the development of their

mesenterial filaments, which are already well developed when the third and fourth pairs of mesenteries have only begun to show (larva A). The mesenterial filaments of the third pair of mesenteries show only after the six pairs of primary mesenteries have reached a comparatively advanced stage of development (Larva I).

The bilateral symmetry of the planula is shown in the position, as well as the order of development, of the six pairs of primary mesenteries. This is clearly shown in the position of pairs *I* and *II*. The two mesenteries of pair *I* lie almost in the same straight line in cross sections, while the mesenteries of pair *II* if produced would meet at an angle of about 45 degrees (Fig. 1, *D;* Fig. 2, *I;* Fig. 4, *F*). Further, if the transverse sections be examined, it will be noted that the length of the circumference on the ventral side between the peripheral ends of the mesenteries of pair *I* is greater than the length of the circumference between the peripheral ends of pair *II*. Both these facts may be expressed by saying that the angle between the mesenteries of pair *I* on the ventral side is greater than the angle between the mesenteries of pair *II* on the dorsal side.

The transverse sections show that in the older larvae the oesophagus is elliptical in cross section and that the long axis of the ellipse is dorsoventral, a condition found in *Manicina areolata* by Wilson ('88). The oesophagus is continued further aborally on the ventral than on the dorsal side.

The mesenterial filaments of mesenteries *I* and *II* are continuous with the ectoderm of the oesophagus and are formed by an aboral growth of this ectoderm. These filaments show the same histological structure as the ectoderm of the outer surface, lacking however nettle cells. The condition found in larva I seems to show that the mesenterial filaments of mesenteries *III* are developed from the endoderm without any connection with the ectoderm.

In *Manicina areolata* Wilson ('88) has shown that the filaments of the first three pairs of mesenteries are developed from the oesophageal ectoderm. In *Aulactinia* McMurrich ('91) found that there was no reflection of the ectoderm as described in *Manicina* by Wilson ('88), and that the median streak (which appears before the lateral streaks) of the filaments of the first three mesenteries was developed from the endoderm.

My preparations seem to show that the gastrovascular cavity in Agaricia is developed by a breaking down and splitting of the endoderm and that the mesenteries, muscle cells, and the cells which will form or have formed the mesenterial filaments are the agents which determine its form.

PART II. ON THE POSTLARVAL DEVELOPMENT.

1. Form of the Young Polyp.

At the time of the flattening out of the young polyp soon after fixation there is no evidence of tentacles. The six pairs of primary mesenteries show clearly as grooves on the surface and when viewed by transmitted light as dark lines. The oral aperture, as in the planula, is oval. The young polyps were not studied in sections as it was desired to preserve the skeletons.

2. The Early Development of the Skeleton.

The study of the skeleton has been confined to the skeletons of the larvae which fixed themselves to the glass vessels in which they were kept. In spite of numerous efforts to rear young polyps and to obtain early stages in the development of the skeleton, only a few skeletons suitable for studying the development of the primary ento-septa were obtained. Two of these have been chosen for description.

a. Description of Skeleton A.

This skeleton (Plate 5, top figure) shows a thin calcareous layer, the basal plate, covering the area of the glass to which the polyp has attached itself. This layer is slightly thickened in the centre, apparently an unusual condition; for a columella is not developed in the older skeletons obtained. The six primary entosepta are arranged radially, extending from near the periphery about half way toward the center. The two entosepta on the left and the upper one on the right show forking at their peripheral ends. The basal plate is thickened near the entosepta in areas corresponding to the primary entocoels. A thin outer ring which extended round the basal plate was largely destroyed in the maceration, a small part of it is shown in the lower part of the photograph. It surrounded the outer limit of the soft tissues of the polyp. The opacity of the young polyp made it impossible to study the relations of the skeleton to the soft parts while the animal was still alive. So an outline drawing was made of the

living polyp showing the positions of the mouth and mesenteries. When the polyp was killed and the soft parts macerated it was found that this drawing could be fitted with certainty over a drawing of the skeleton (Fig. 5), owing to the exact correspondence between the periphery of the basal plate and the outline of the soft parts of the polyp. The drawings show that the primary entosepta lie between the primary mesenteries and, when compared with the photograph (Plate 5, top figure), that the thickenings of the basal plate referred to above coincide exactly with the areas enclosed in the primary entocoels.

It will be noticed in both photograph and drawing that the primary

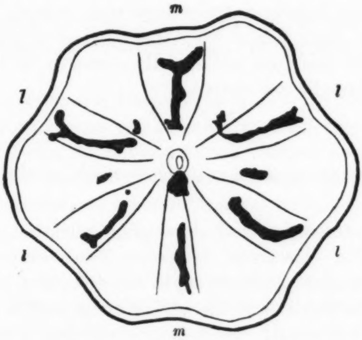

FIGURE 5. *Agaricia fragilis.* Outline drawing of a young polyp, showing the six pairs of primary mesenteries and the opening of the mouth, superposed on a drawing of the skeleton of the same polyp (septa in solid black) made separately after the polyp had died and disintegrated. *m*, *m*, median septa, *l*, *l*, lateral septa.

septa show bilateral symmetry in their arrangement and form. Unfortunately it was not possible in the living polyp to distinguish a dorsal from a ventral side. That the axis of this symmetry is, however, dorso-ventral is shown by the oral aperture, which has its long axis in this direction. The axis of symmetry is occupied by two entosepta, which will be called median (Fig. 5, *m*); the upper (in the figure) lateral septa (*l*) make equal angles with the median plane. This is also true of the lower lateral septa, but the angle which the latter make is less than that made by the upper septa. All four of these septa are concave toward the upper side of the figure.

Both photograph and drawing show two pairs of very small exosepta. Owing to ignorance as to which of the median septa is dorsal, it is not possible to say whether the upper pair is the dorso-lateral or ventro-lateral pair. The photographs and drawing have been oriented, however, to correspond with the arrangement found by Duerden (:04) in *Siderastrea radians,* where the dorsal septa are the first to develop.

b. Description of Skeleton B.

In this skeleton a distinct epitheca surrounds the basal plate. The entosepta are relatively larger than those of skeleton A. There is the same bilateral symmetry with regard to the angles which the lateral septa make with the median plane. The lateral septa, however, in this case are slightly concave on the lower side. Exosepta and columella are absent.

c. Conclusions on the Early Development of the Skeleton.

The early skeletons obtained show great variation in size and in the development of the septa. In some cases only five septa are developed, in others one or more septa are defective. This variation may be due to the fixation of the larvae at an earlier period in their development than is usual; the skeletons showing most variation are the smaller ones.

The following conclusions may however be drawn. The basal plate and the six primary entosepta are the first structures to be developed. The primary exosepta do not arise simultaneously. Bilateral symmetry is frequently shown in the arrangement of the primary entosepta.

Four possible explanations of this bilateral symmetry occur to the writer. (1) The polyps which formed these skeletons may have fixed themselves with the dorsal or possibly ventral side bent over toward the substratum. (2) One or more of the median entocoels may have been enlarged by the growth of the wall of the polyp in that region. (3) It may represent a persistence of the bilateral symmetry seen in the development of the mesenteries. (4) It may represent the tendency of the coral to grow upward at one point to form the frond-like corallum of the older coral.

d. Stage with Twelve Primary Septa.

A number of skeletons in this stage were obtained (Plate 5, bottom photograph). They show six primary entosepta and six exosepta. The epitheca covers the outer portion and is in the form of the base of a cone. It is decorated with ridges running toward the oral end of the polyp. The theca is seen joining the entosepta and exosepta. The primary entosepta extend beyond the theca but do not reach the epitheca. In a few of the skeletons a slight indication of the bilateral symmetry described for the earlier skeletons could still be recognized.

3. Comparison of the Development of the Skeleton in Agaricia fragilis with that in other Hexacorallidae.

In *Astroides calycularis* Lacaze-Duthiers ('73) found that each of the six primary entosepta was formed from three centres of calcification, the septa being in consequence Y-shaped with the upper part of the Y toward the periphery. The two septa on the left in Plate 5 (top figure) are forked at their peripheral ends, although the prongs of the fork are not so large as in *A. calycularis*. Lacaze-Duthiers found that the other septa appear irregularly. The same species has been studied by Koch ('82), who also finds the primary septa forked. Both these authors find that the primary entosepta are developed before the theca or epitheca.

In *Caryophyllia cyathus* and *C. clavus* Lacaze-Duthiers ('97) found similar stages in the development.

In the development of *Siderastrea radians*, studied by Duerden (:04), six primary entosepta are developed as single continuous rods without connection with the theca or epitheca. An outer ring, the beginning of the epitheca, similar to the ring described in skeleton A, surrounds the basal plate. The primary exosepta are developed in dorso-ventral succession and independently of the entosepta.

University of Wisconsin,
April, 1915.

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Description of Plates.

Plates **1–6**. Development of *Agaricia fragilis*. All, except top and bottom figures of Plate **5**, are photomicrographs of transverse sections of free swimming larvae. $\times$ 175.

Plate **1**. Larva A, upper photograph, section 15; lower, section 24.

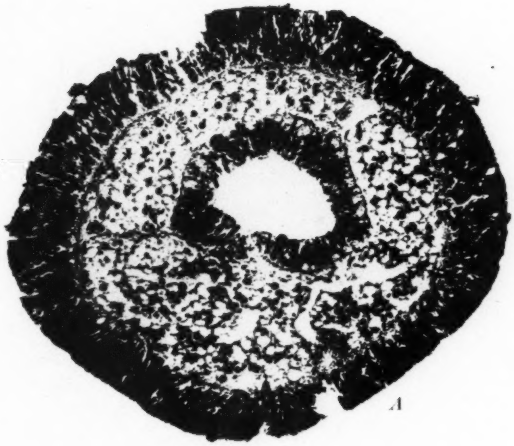
Plate **2**. Larva A, upper photograph, section 30; lower, section 46.

Plate **3**. Larva F, upper photograph, section 12; lower, section 17.

Plate **4**. Larva F, upper photograph, section 61; lower, section 73.

Plate **5**. Two middle figures are of Larva I, the left (*C*) being section 19; the right (*D*), section 26. The top figure (*A*) is a photograph of skeleton A, the bottom one (*B*) of skeleton C.

Plate **6**. Larva I, upper photograph, section 73; lower, section 93.



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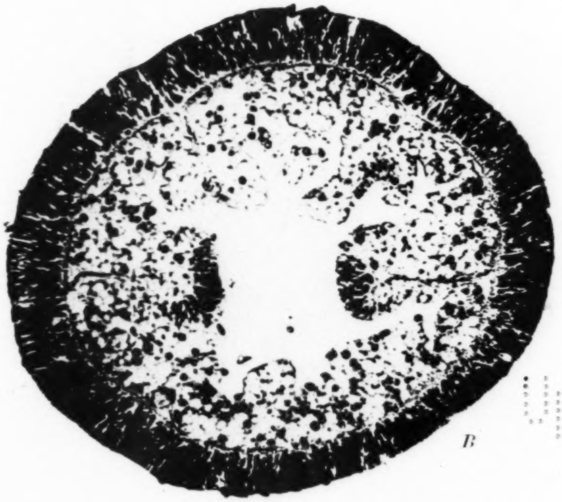

B

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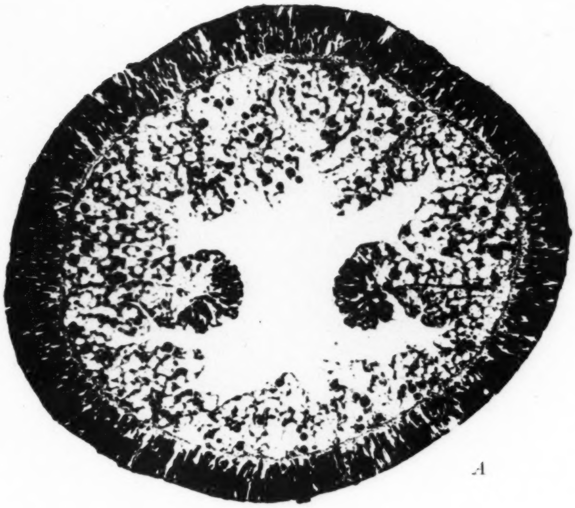

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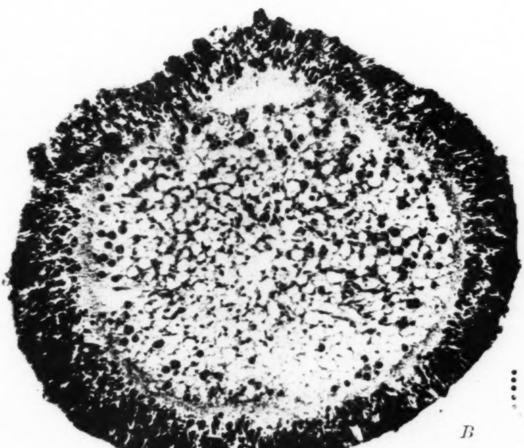

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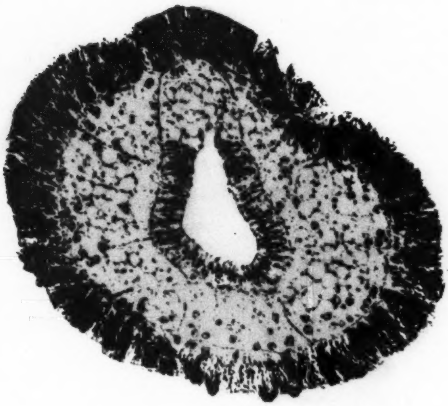

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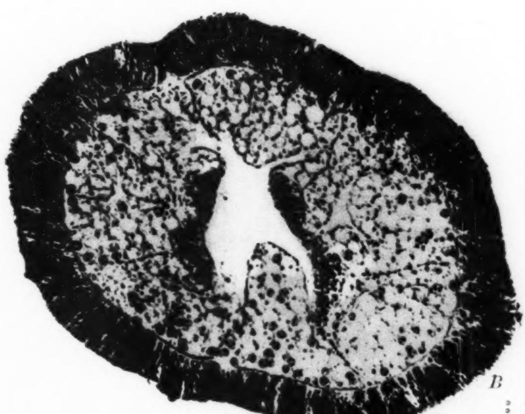

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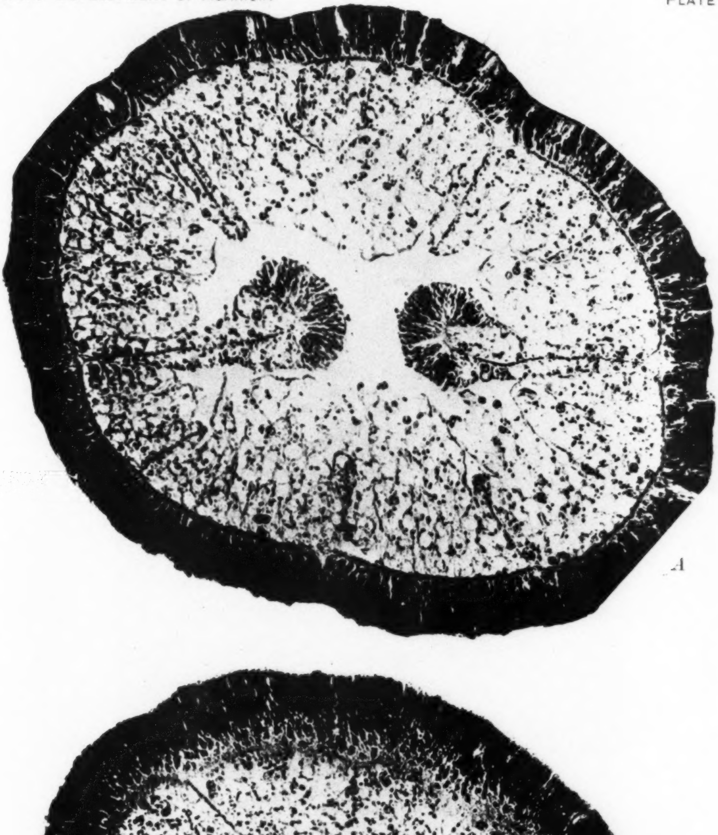
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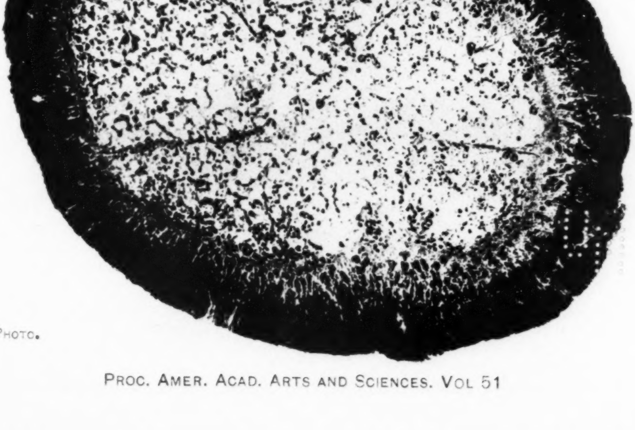
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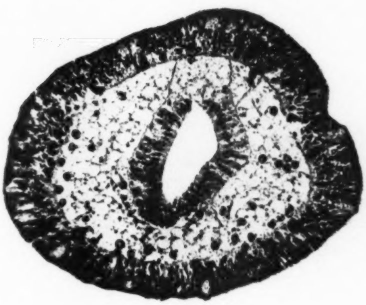

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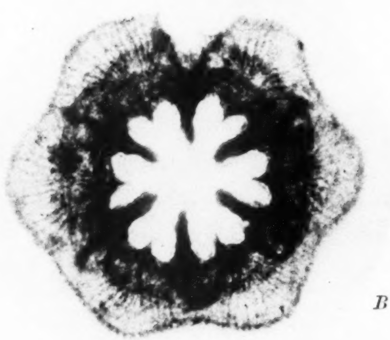

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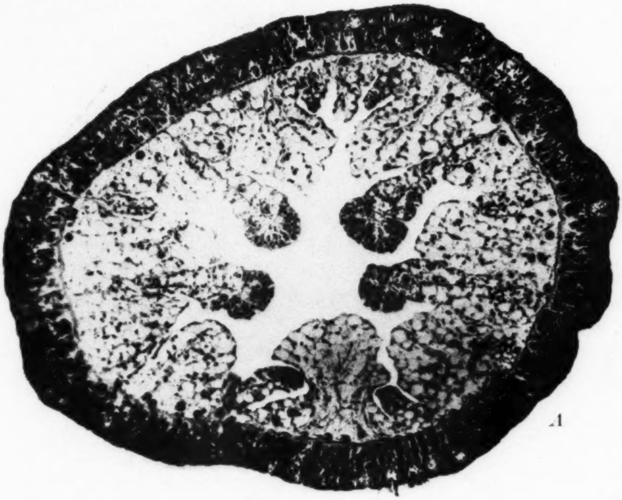

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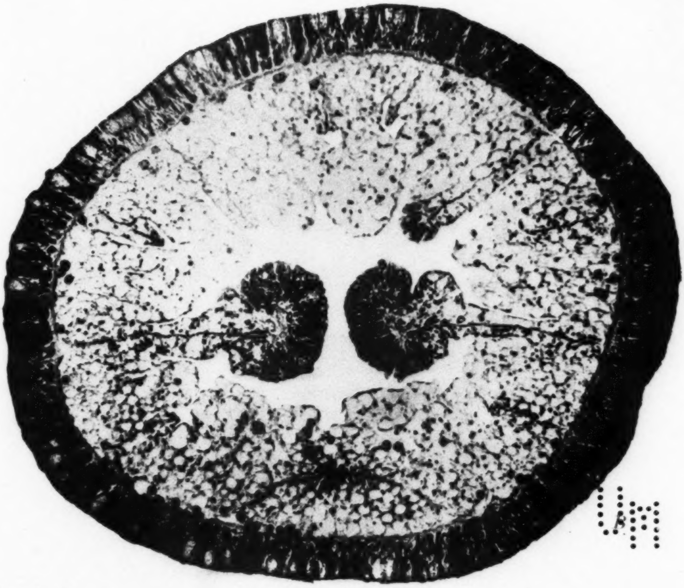

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